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Permian Gastropods from Perak, Malaysia
Part 2. The Trochids, Patellids, and Neritids

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Gastropods from Perak, Malaysia Part 2. The Trochids, Patellids, and Neritids

ROGER L BATTEN[1]

ABSTRACT

This is a continuation of a study of Permian gastropods from the *Misellina claudiae* zone from the H. S. Lee Mine no. 8 near Kampar, Perak, Malaysia. The fauna constitutes one of the richest, most diverse, known in the Permian, providing a critical base in the eastern Tethys. New species of *Sallya* Yochelson, 1956, and *Dichostasia* Yochelson, 1956, record their presence for the first time outside of the west Texas region. One species of patellids is recorded, 10 species of trochids, four new, and nine species of neritids, three new, are described. Most of the neritids are similar to morphotypes found from Djebel Tebaga east to Mongolia. Key characters in *Trachydomia imbricata*, new species, suggest an ancestral relationship to *Neritopsis*. Wall ultrastructure is reported and discussed for *Trachyspira delphinuloides* Gemmellaro, 1889, and for the Recent *Neritopsis radula* Linné, 1758.

INTRODUCTION

This study is a continuation of the description of the Permian Malaysian gastropods. It is based on the marine molluscan fauna found at a single locality, Lee Mine no. 8 near Kampar, Perak (Map of Malaysia sheet 2n/9 old series, [MR 90356], see Batten, 1972, p. 5 for details). The fauna is dominated by gastropods but corals, scaphopods, bivalves, brachiopods, and cephalopods are present along with fusulinids and other Foraminifera. Based on fusulinids, the unnamed white-colored limestone is dated as Late Artinskian-Early Guadalupian (Jones, Gobbett and Kobayashi, 1966, p. 328), and is included as a part of the *Misellina claudiae* zone. As mentioned in the earlier study, this fauna is, with one exception, the richest known in the Permian.

Two genera, *Sallya* Yochelson, 1956, and *Dichostasia* Yochelson, 1956, are included here because they are trochid-like in appearance; they belong to the superfamilies Pseudophoracea and Caspedostromatacea, respectively. These superfamilies have been thought to be problematic and probably polyphyletic. It has not been possible in the past to assign them to any known order. They generally are placed in the Archeogastropoda with a query (Knight, Batten and Yochelson, 1960). I would be inclined to refer them, as aberrant groups, to the Suborder Trochina. Until a thorough analysis of these groups are made, I provisionally accept them as being internally consistent on morphological grounds. This would be particularly apropos for the Pseudophoracea since some of

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the genera have been reported to have nacre (Knight, Batten and Yochelson, 1960, p. 297). *Sallya* and *Dichostasia* are of particular interest from the paleobiogeographical view because they were originally described from the Permian of the west Texas region and were previously known only from that region. This disjunct distribution was noted in the case of two pleurotomarian genera, *Lacunospira* Batten, 1958, and *Lamellospira* Batten, 1958. It is interesting to note that the four genera in question are highly unique forms. Further, the species between the two areas are remarkably similar in details.

The patellids are represented by a single specimen of the genus *Lepetopsis* Whitfield, 1882, reflecting the fact that, in general, the patellids are not a common element in Upper Paleozoic faunas.

The neritacean species are similar to those found in the Sosio beds of Sicily, the Permian of Timor and Sumatra, the Salt Range of Kashmir, Yunnan, Mongolia, the Djebel Tebaga of southern Tunisia, and the west Texas Permian and can be identified as typical of the Tethyan faunal realm. The neritacean genus *Trachydomia* Meek and Worthen, 1866, is widespread in distribution and is known from many Upper Paleozoic faunas. It is not particularly abundant except in the Djebel Tebaga (see Termier, Termier and Vachard, 1977) and the Sosio faunas. The earliest reported occurrence of *Trachydomia* is in the Lower Pennsylvania of the midwestern United States. It was probably derived from some group like the Lower Carboniferous *Turbinitella* de Koninck, 1881, which shares such characters as a concave subsutural ramp and a thickened apertural lip with a concave trough.

Two species of *Trachydomia* resemble the Triassic genera *Hungariella* Kutassy, 1934, and *Neritopsis* Grateloup, 1832. The latter genus is represented today in the Indo-pacific fauna by a single species *N. radula* (Linné), 1758, the only extant species of the family Neritopsidae; this family includes 14 extinct genera distributed primarily in the Late Paleozoic and Mesozoic. *Neritopsis* must have been derived from an ancestor very close to that of *Trachydomia imbricata*, new species; the details of the complex lamellate ornament are identical (see fig. 21) as well as the formation and development of primary noding, the construction of the apertural complex and the early development of the basic ornament pattern. The details of ornament and the basic apertural design in some of the variant patterns of *T. gobbetti*, new species, suggests that the morphotype represented by this species could also have been the source for *Hungariella*.

Trachyspira Gemmellaro, 1889, on the other hand, is primarily known from the Middle Permian Sosio beds where five species have been described. The genus is represented in the Malaysian sample by 12 specimens of *T. delphinuloides* Gemmellaro, 1889, and is moderately abundant in the Djebel Tebaga. The only other occurrence of *Trachyspira* that I am aware of is from the Middle Permian of the west Texas region.

Finally, the radiation of the Neritopsidae during the middle Permian and into the Triassic parallels that of the early radiation of the caenogastropods which is first encountered in the Malaysian fauna. In the latter radiation, a number of neomorphs appear in the Malaysian fauna which are the earliest representatives of several important Mesozoic groups first encountered in the Mid to Upper Triassic (the families Coelostylinidae, Procerithiidae, Potamididae (?) and Nerineidae).

Naticopsis M'Coy, 1844, is represented by four species belonging to four of eight morphotypes recognized in the Middle American Pennsylvanian (see Knight, 1933, pp. 366-367). These species are in the middle of the morphological spectrum of the genus and are difficult to treat owing to a paucity of distinctive features. Most Permian species seem to be fairly restricted to given sub-provinces of the Tethys. For example, *N. depressa* (Guembel), 1877, has only been reported from the Bellerophonkalk and associated strata in Europe. *N. khurensis* Waagen, 1880, is widely reported from central Asia; at Karakorum and the Salt Range; from Malaysia to Sumatra and north through Yunnan and Kweichow to Mongolia.

As mentioned in an early report of the Malaysian pleurotomarians (Batten, 1972, p. 5), the preservation of the fauna is unusual in that specimens are powdery and fragile and mainly natural casts. They are found in a matrix of decomposed limestone partly resulting from baking by an intrusive underlying the mine.

Batten (1972, p. 5) stated that no wall ultrastructure was found in the pleurotomarians, suggesting that the specimens were natural casts. While examining the sample of *Trachyspira delphinuloides* Gemmellaro, 1889, it was found that several specimens showed some ultrastructure preserved (see fig. 32). The structure was observed on a freshly broken portion of the adult whorl and not on breaks that occurred before lithification of the lime mud when the broken surface could have been impressed into the mud to form a mold, which subsequently could have been filled by secondary calcite. SEM examination revealed that the wall is composed of a single massive complex prismatic layer reminiscent of the wall found in *Bellerophon* Montfort, 1808 (see MacClintock, 1967, pp. 94-107). The apices of the prisms undulate with the growth lines, indicating that there is no outer layer of wash formed by the mantle.

I was unable to obtain specimens of the Triassic species of *Neritopsis* but I sectioned the Recent species *N. radula* (Linné), 1758, which is composed of the relatively thin outer spiral crossed-lamellar layer and an inner collabral crossed-lamellar layer, having the same characteristics as that of the outer layer (see fig. 33). The tops of the first order lamellae form the inner surface of the shell in the same manner as the prisms form the surface of *Trachyspira*. Since I believe that *Neritopsis* was derived from *Trachydomia* it is difficult to accept the fact that two different types of ultrastructure could be present in closely related genera. Complex prismatic and crossed-lamellar structure is found in a number of primitive molluscs such as the bellerophontids, where genera in the same family have both structures. I speculate that in those forms that have crossed-lamellar structure, it was derived from, or can be transformed from, a complex prismatic structure. Based on observations within more advanced groups, there is consistency of wall structure within each group (even at the superfamily level). It would not be likely to find these different types in the same subfamily. The problem is not soluble at present.

As defined here, a morphotype is a relative term describing a group of specimens, usually a species, possessing a distinct set of characters which recur in different groups in space and/or time, allowing for convergence but without implying, necessarily, direct genetic relationships.

ACKNOWLEDGMENTS

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The following abbreviations are used: AMNH, American Museum of Natural History; H, shell height, in most cases this measurement is approximate because one or more of the early whorls are missing; SEM, Scanning Electron Microscope; SD, subsequent designation; SP, ANG, the spiral angle of the shell; W, shell width.

SYNOPTIC CLASSIFICATION

Class Gastropada
- Subclass Prosobranchia
  - Order Archeogastropoda
    - Suborder Patellina
      - Superfamily Patellacea
        - Family Metoptomatidae Wenz, 1938
          - *Lepetopsis* sp. . . . . (1)[a]

[a]Numbers in parentheses are sample sizes.

Suborder Trochina	
Superfamily Platyceratacea	
Family Holopeidae Wenz, 1938	
Subfamily Gyronematidae Knight, 1956	
Yunnania meridionalis Mansuy, 1914	(15)
Yunnania sp.	(1)
Superfamily Microdomatacea	
Family Microdomatidae Wenz, 1938	
Microdoma variegata, new species	(22)
Microdoma nodosum, new species	(2)
Family Elasmonematidae Knight, 1956	
Anematina sp.	(4)
Superfamily Anomphalacea	
Anomphalus sp.	(34)
Turbonilopsis rotunda Delpey, 1916	(5)
Superfamily Pseudophoracea	
Family Pseudophoridae Miller, 1889	
Sallya terendaka, new species	(2)
Superfamily Craspedostomatacea	
Family Craspedostomatidae Wenz, 1938	
Subfamily Dichostasinae Yochelson, 1956	
Dichostasia kampari, new species	(13)
Suborder Neritopsina	
Superfamily Neritacea	
Family Neritopsidae Gray, 1847	
Subfamily Naticopsinae Miller, 1889	
Naticopsis (Naticopsis) piriformis Mansuy, 1912	(3)
Naticopsis (Naticopsis) khurensis Waagen, 1880	(7)
Naticopsis (Naticopsis) praealta Wanner, 1922	(7)
Naticopsis (Naticopsis) tschernyschewi Yakowlew, 1889	(5)
Subfamily Neritopsinae Gray, 1847	
Trachydomia gobbetti, new species	(23)
Trachydomia dussaulti Mansuy, 1913	(2)
Trachydomia imbricata, new species	(49)
Trachydomia gemmulata, new species	(3)
Trachyspira delphinuloides Gemmellaro, 1889	(12)
Total specimens studied	188

SUBORDER PATELLINA

SUPERFAMILY PATELLACEA

FAMILY METOPTOMATIDAE WENZ, 1938

GENUS *LEPETOPSIS* WHITFIELD, 1882

TYPE SPECIES: *Patella levettei* White, 1882, p. 359.

Lepetopsis sp.
Figure 1

DISCUSSION: The single specimen in the fauna which belongs to this genus is poorly preserved. Faint, irregular lines suggest a concentric ornament pattern. The apex is near the center of the rather high patelliform shell. This shell shape serves to separate the specimen from such described Tethyan Permian species as *L. dainellii* Greco, 1937, *L. stefaninii* Greco, 1937, or *L. petsus* Mansuy, 1913, all of which are quite low in profile.

SPECIMENS: 1.

MEASUREMENTS: Figured specimen AMNH 40840: SP ANG 73 degrees, H 8.5. mm, W 14.5 mm.

SUBORDER TROCHINA

SUPERFAMILY PLATYCERATACEA HALL, 1859

FAMILY HOLOPEIDAE WENZ, 1938

SUBFAMILY GYRONEMATINAE KNIGHT, 1956

GENUS *YUNNANIA* MANSUY, 1912

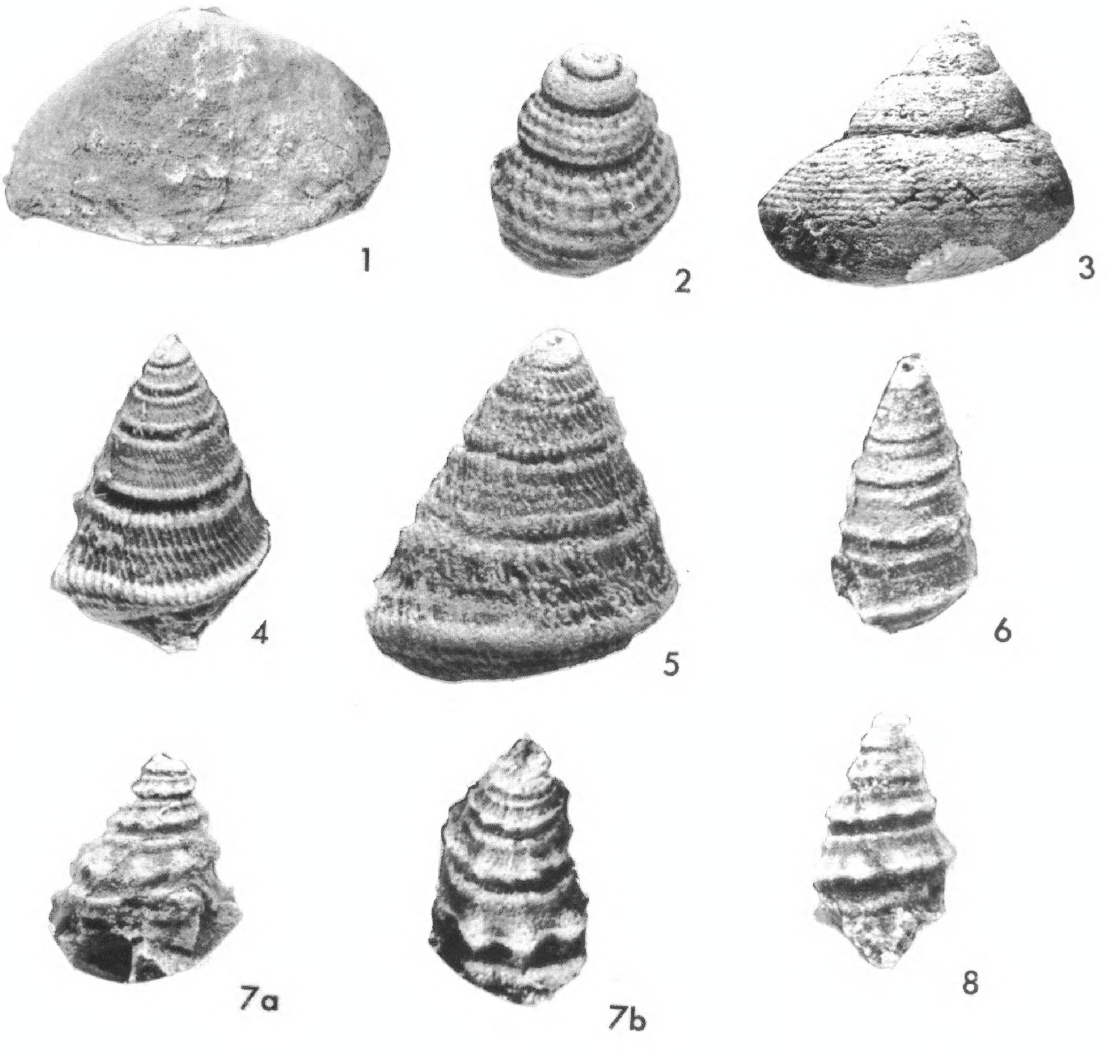
TYPE SPECIES: *Y. termieri* Mansuy, 1912, p. 104, pl. 18, fig. 20 (SD Cossmann, 1918, p. 327).

DISCUSSION: The chief distinguishing features of species attributed to *Yunnania* are the globose whorl with dominant spiral ornament and a moderately high-spired shell. The name has been rather loosely applied, in my opinion, to any Upper Paleozoic trochid-like form having these features. For example, Licharew (1967), assigned a relatively low-spired species *(Y. semigranulosa)* with inflated whorls to the genus. At present there is no way to resolve the problem of morphological limits, since the genus is not well represented in most Upper Paleozoic faunas.

Yunnania meridionalis Mansuy, 1914

Figure 2

Yunnania meridionalis Mansuy, 1914, p. 41, pl. 4, fig. 10



FIGS. 1-8. 1. *Lepetopsis* sp., AMNH 40840, oblique side view, note apex near center of shell, X3. 2. *Yunnania meridionalis* Mansuy, 1914, AMNH 40842, oblique side view, X10. 3. *Yunnania* sp., AMNH 40841, side view, X1. 4. *Microdoma variegata*, holotype, AMNH 40845, oblique side view, X10. 5. *Microdoma variegata*, paratype, AMNH 40849, slightly oblique side view, note wider whorls compared to holotype, X10. 6. *Microdoma variegata*, paratype, AMNH 40846, oblique side view, note narrow whorls and reduced ornament, X10. 7a. *Microdoma nodosum*, holotype, AMNH 40852, side view, X10. 7b. Oblique top view showing growth lines on earlier whorls, X10. 8. *Microdoma nodosum*, paratype, AMNH 40853, side view showing narrow shell and more numerous nodes than the holotype, X10.

Yunnania meridionalis Mansuy: Delpey, 1941, p. 274, fig. 16

DESCRIPTION: Trochiform shells with strongly developed cancellate ornament; first several whorls unornamented, low-spired; upper whorl surface somewhat flattened; whorls inflated, sutures embracing just below rounded periphery; spiral cords dominant, five or more cords on whorl evenly spaced except at periphery; six or seven spiral cords on base less well developed than on whorl; collabral ornament rounded, elongated nodes on spiral cords, strongest near suture, disappearing beneath periphery; base rounded, anomphalus; spiral cord marks funnel-like umbilical depression; columella lip straight, reflexed on parietal surface.

DISCUSSION: The 15 small shells in this sample are immature, having five or six whorls compared to the seven or eight whorls in the Cambodian fauna described by Delpey. This sample falls well within the morphological range of Mansuy's and Delpey's descriptions. This species differs from others by having somewhat coarser spiral ornament and rather well-formed nodes concentrated near the suture.

The most unique character complex of this sample is the nature of the early whorls. In some specimens they are much larger than would be expected on a normal orthostrophic shell, and the first several whorls are nearly planispiral. This complex is less noticeable in other specimens. Variability is also reflected in the placement of the theoretical point of origin of the log spiral. In a regular orthostrophic shell the point of origin approximately coincides with the top of the protoconch. On one specimen measuring 2.7 mm. in length, the point of origin lies 0.5 mm. above the protoconch. The spiral angles range from 58 degrees to 79 degrees. The whorl profile also shows a moderate degree of variability. The upper portion of the whorl is somewhat flattened, but it may be quite evenly rounded as in the type specimen and similar to that illustrated by Delpey (1941, p. 274, fig. 16). Ornament variation is moderate, involving relative development of the spiral cords near the periphery in the region where sutural contact is most likely. Intercalated spiral threads may form between the cords, usually in the peripheral region and on the base. As Delpey (1942, p. 275) pointed out a similar morphotype is described from the Visean by de Koninck as *Portlockia subcancellata*. Licharew (1967, pl. 10, figs. 1-5) has described the same morphotype from the Carboniferous of Ferghana as *Yunnania romanovskyi* which has a slightly flattened upper whorl surface. However, the cancellate ornament extends down below the periphery on the base.

SPECIMENS: 15.

MEASUREMENTS: AMNH 40841: SP ANG 52 degrees, H 2.5 mm., W 2.2 mm.; AMNH 40842: SP ANG 90 degrees, H 4.3 mm., W 4.5 mm.; AMNH 40843: SP ANG 50 degrees, H 2.3 mm., W 2.1 mm.

Yunnania sp.
Figure 3

DESCRIPTION: Large shell with inflated whorls; semi-angulate periphery low on whorls; sutural contact at periphery; about 14 evenly spaced spiral cords on adult whorls above periphery; spiral cords beaded owing to collabral interference ornament; collabral growth lines visible between spiral beads but ornament not developed between adjacent beads: base not well preserved presumably without ornament; anomphalus, with a raised funicle exaggerated by bordering depressions.

DISCUSSION: This single specimen extends the concept of *Yunnania* by virtue of the angulate whorl profile. All species assigned to *Yunnania* thus far tend to have globose whorls and are relatively high-spired (with the exception of *Y. semigranulosa* mentioned above). This specimen differs from those Carboniferous specimens assigned to *Y. semigranulosa* in having the angulate whorl profile and lacking a flattened platform immediately adjacent to the suture. *Yunnania semigranulosa* appears to have the sutural contact somewhat higher on the whorl. Further, *Y. semigranulosa* has unevenly developed spiral cords and a base with spiral cords which appears to have a very fine overlay of collabral threads. Most species of *Yunnania* tend to have some variety of cancellate ornament.

SPECIMENS: 1.

MEASUREMENTS: AMNH 40844: SP ANG 85 degrees, H 15.08 mm., W 9.56 mm.

SUPERFAMILY MICRODOMATACEA WENZ, 1938

FAMILY MICRODOMATIDAE WENZ, 1938

GENUS *MICRODOMA* MEEK AND WORTHEN, 1867

TYPE SPECIES: *Microdoma conicum* Meek and Worthen, 1867, p. 269.

DISCUSSION: Two species have been reported from the Permian, *Microdoma imbricata* Mansuy, 1921, was described from the *Spiriferina cristata* beds of Eastern Yunnan and *M. biserratum* Mansuy, 1912, (not Phillips, 1836) from Eul-Kay, Yunnan. *Microdoma imbricata* does not fall within the morpholgical range of the genus; for example, the log spiral expands much more rapidly than it does in any other known species. The whorls of *M. imbricata* are more globose and there is a lack of collabral noding on the periphery, a rather consistent feature within the genus; a mid-whorl shoulder is also present.

Microdoma imbricata probably should be placed in some genus of the Platyceratacea. *Microdoma biserratum* (Phillips) Mansuy, 1920, is conspecific with *M. variegata*, new species, for reasons given below but differs from the type and concept of *M. biserrata* Phillips, 1836.

Microdoma variegata, new species
Figures 4-6

Microdoma biserrata (Phillips): Mansuy, 1920, p. 33.

DIAGNOSIS: Moderately high to high-spired turbiniform shells with noded peripheral and sutural cords; one to four spiral threads on flat to gently concave whorl face; collabral threads form interference nodes with spiral ornament; whorls embrace at or below periphery; base flatly rounded with five or more noded spiral cords; anomphalus or narrowly phaneromphalus; ornament resorbed on parietal surface.

DISCUSSION: This species, like others in the genus *Microdoma*, is highly variable in a number of features (see Batten, 1966, p. 55). The most obvious variation involves the general appearance of the shell which may be almost equiangular in outline, to a tall narrow, stepped shell. If the shell has the former appearance, the whorls embrace at, or close to, the periphery, the peripheral and sutural cords are reduced and the whorl face, as well as the base, is almost flat. Higher spired shells have the two noded spiral cords well developed, giving the whorl face a more concave shape. A few specimens show slight uncoiling in the final whorl.

Collabral ornament can vary from unevenly to evenly spaced and well-developed cords or threads to narrow nodes on spiral elements without expression, (see figs. 4-6). Spiral ornament on the whorl surface (exclusive of the peripheral and sutural cords) consists of from one to four unevenly spaced and developed threads. If there is just a single thread, it tends to be in the center of the whorl face. Heavier development of the spiral elements tends to be associated with higher spired shells. The spiral cords on the base are strong and evenly formed and display less variation. There does not seem to be any relationship between an open or closed umbilicus and any other feature such as whorl shape or tightness of coil which are usually correlated with umbilical development. All of this ornament variability with differing frequencies of expression is found in such Carboniferous species as *M. bicrenulata* (De Koninck), 1883, from western Europe.

Microdoma variegata is most similar to the Carboniferous *M. biserrata* (Phillips), 1836, in shell shape, emphasis of ornament, and position of whorl embracement. It differs in having a well formed sutural cord, multiple spiral threads on the whorl surface and spiral cords on the base. Mansuy (1920, p. 33) attributed his specimen from Eul-Kay, Yunnan, to *M. biserrata* but his illustrations shows that it is conspecific with *M. variegata*.

SPECIMENS: 22.

MEASUREMENTS: Holotype, AMNH 40845: SP ANG 44 degrees, H 4.1 mm., W 2.6 mm.; Paratype AMNH 40846: SP ANG 29 degrees, H 3.4 mm., W 1.8 mm., Paratype AMNH 40847: SP ANG 56 degrees, H 4.6 mm., W 3.6 mm.; Paratype AMNH 40848: SP ANG 45 degrees, H 4.3 mm., W 4.0 mm.; Paratype AMNH 40849 b: SP ANG 60 degrees, H 4.2 mm., W 3.5 mm.; Paratype AMNH 40850 c: SP ANG 57 degrees, H 2.3 mm., W 2.0 mm.; Paratype AMNH 40851 d: SP ANG 45 degrees, H 5.0 mm., W 3.2 mm.

ETYMOLOGY: from the Latin *varius*, change.

Microdoma nodosum, new species
Figures 7a, 7b; 8

DIAGNOSIS: Moderately high-spired shells with heavily noded spiral ornament; nuclear whorls unknown; early whorls with reduced ornament; sutures placed on periphery; sutural cord with widely spaced, weakly formed nodes; peripheral spiral cord with rounded nodes; dominant mid-whorl cord with very large rounded nodes; mid-whorl nodes lineated between whorls, appearing varix-like; whorl face slightly concave; base apparently flattened, umbilicus not preserved.

DISCUSSION: Two broken specimens are sufficiently well preserved to recognize them as being a highly distinctive new species of *Microdoma*. Primary noding is a common phenomenon with the genus, but with the exception of *M. nodosum* and *M. serrilimba* (Phillips) 1836, it is restricted to the peripheral and sutural spiral elements. *Microdoma serrilimba*, from the Carboniferous of Derbyshire, has a noded mid-whorl spiral cord about as well developed as the sutural cord and peripheral cords in contrast to *M. nodosum* where the mid-whorl cord and accompanying nodes are the strongest in development. Additionally, *M. serrilimba* is higher-spired and the nodes are not aligned to give a varix-like appearance as in *M. nodosum*. I have not been able to identify this morphotype in any other fauna.

SPECIMENS: 2.

MEASUREMENTS: Holotype AMNH 40852: SP ANG 41 degrees, H 2.3 mm., W 1.9 mm.; Paratype AMNH 40853: SP ANG 43 degrees, H 2.2 mm., W 1.8 mm.

ETYMOLOGY: Nodosum from the Latin *nodus*, knot.

FAMILY ELASMONEMATIDAE KNIGHT, 1956

GENUS *ANEMATINA* KNIGHT, 1933

Anematina sp.
Figure 9

TYPE SPECIES: *Anematina proutana* (Hall), 1858, p. 30.

DISCUSSION: The four specimens, which I am provisionally placing in *Anematina*, are not well enough preserved to display such critical morphology as growth lines. However, several repaired breaks on the shell and a partly preserved aperture indicated that the growth increments were nearly parallel to the axis of the shell. The protoconch and first whorl are flat. The whorl profile is slightly rounded in other whorls and with a slightly angular periphery at mid-whorl. The base is elongate and is narrowly phaneromphalus to hemiomphalus, rounded. The aperture has a reflexed columellar lip. The sutures embrace just above the base.

On the best preserved specimen, there appears to be faint spiral and collabral threads and on the final whorl there are sutural rounded nodes. These ornamental features are not present in described species of *Anematina*, with the exception of *A. proutana* that has spiral threads restricted to the base. Variation between the specimens involves height of spire, sutural embracement and relative whorl inflation.

SPECIMENS: 4.

MEASUREMENTS: AMNH 40856: SP ANG 56 degrees, H 5.0 mm., W 3.2 mm.

SUPERFAMILY ANOMPHALACEA WENZ, 1938

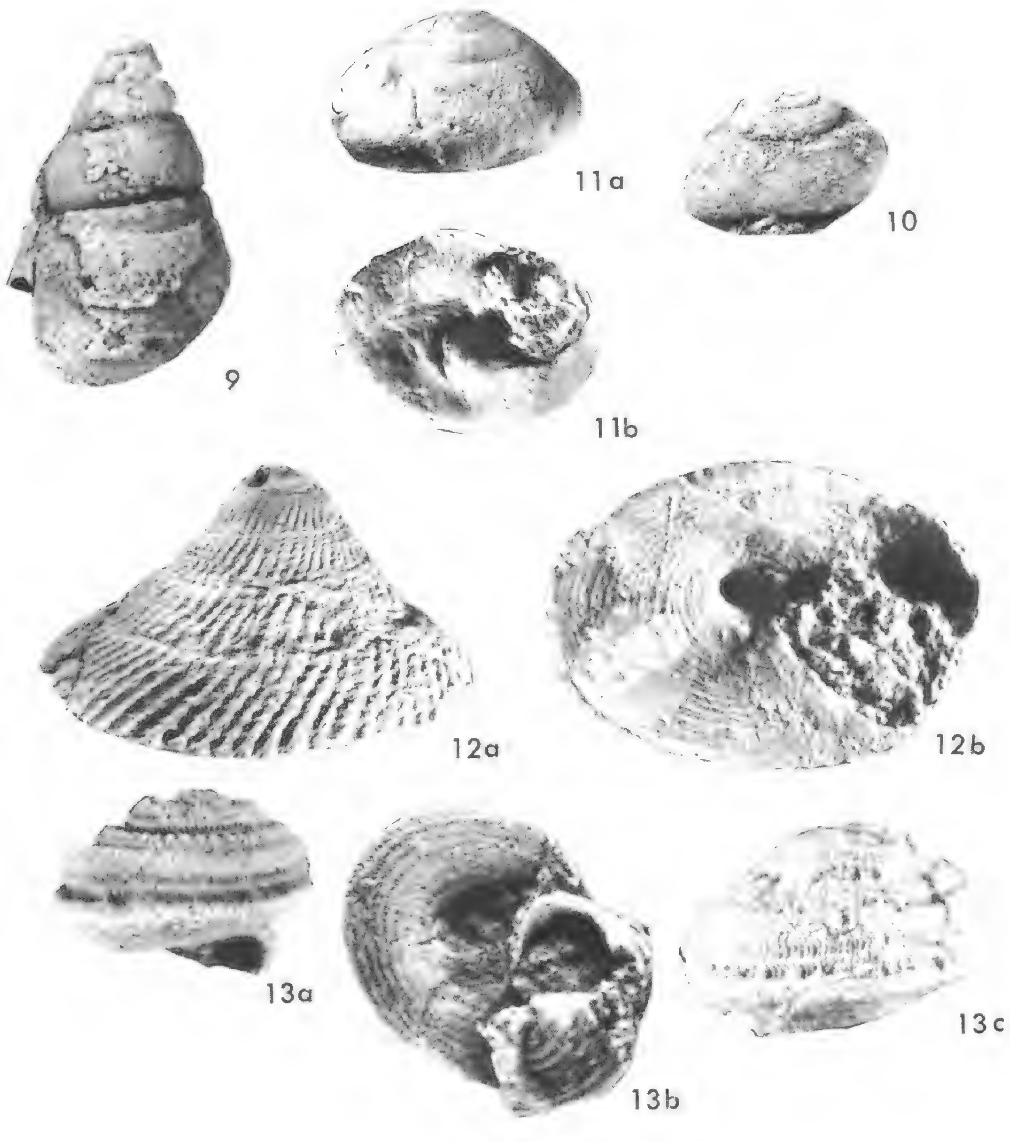
FAMILY ANOMPHALIDAE WENZ, 1938

GENUS *ANOMPHALUS* MEEK AND WORTHEN, 1867

TYPE SPECIES: *Anomphalus rotulus* Meek and Worthen, 1867, p. 268.

Anomphalus sp.
Figures 10-11a, 11b

DISCUSSION: I have isolated several groups of specimens which can be accommodated in this family. Most are poorly preserved but their general shell and whorl shapes and the presence of an umbilical callus or funicle indicate placement in this genus. Two Upper Paleozoic genera of anomphalids, *Anomphalus* and *Turbinilopsis* de Koninck, 1881, have features similar to the Malaysian forms. The type species of *Anomphalus* is low-spired and almost flat on the upper shell surface with whorls overlapping so that the sutures are close together. The whorl shape is evenly inflated. A number of species have been assigned to this genus, dis-



FIGS. 9-13. 9. *Anematina* sp. AMNH 40854, side view of high-spired form, X9.3. 10. *Anomphalus* sp., AMNH 40857, oblique side view showing the angulate, low periphery, X12.7. 11a. *Anomphalus* sp., AMNH 40858, side view showing a rounded, ill-defined periphery, X1.75. 11b. Oblique basal view, note comma-shaped funicle, X1.75. 12a. *Sallya terendaka*, holotype, AMNH 40859, slightly oblique side view, note varix-like noding, X2.1. 12b. Oblique basal view, X2.1. 13a. *Dichostasia kampara*, holotype, AMNH 40861, side view, X8.5. 13b. Oblique basal view, X9.3. 13c. Paratype, AMNH 40862, side view showing collabral ornament and growth lines, X9.3.

playing a considerable amount of variation of umbilical features and whorl shapes. Species such as *A. umbilicatus* Knight, 1933, have a somewhat angulate whorl profile with a broad periphery located low on the whorl. In these species the whorls are less tightly coiled and the axial translation is more pronounced, giving the shell a low-spired profile. These features

are present in one of the isolated groups mentioned above.

The type species of *Turbinilopsis, T. inconspicula,* has a more globular and rounded whorl profile and the sutures embrace lower on the whorl, giving the shell a somewhat higher-spired appearance than in species of *Anomphalus*. Another group of specimens in the Malaysian fauna is of this form.

The central problem with these two genera is a notable lack of characteristics. The few morphological features available are variable so that no clear statement can be made. This is forcefully pointed out by examining the specimens in our samples. There appears to be an almost complete transition between the extremes of the two type species mentioned above. Poor preservation prevents formal recognition of the two groups.

One of the intermediate specimens seems to show faint spiral striae. If this observation is correct, it is an unusual feature for the anomphalids, for if ornament is present, it is usually axial or collabral. ?*Turbinilopsis* sp. illustrated by Mansuy (1914, pl 4, fig. 11) resembles the larger specimens in our sample which are relatively low-spired. *T. rotundus* Delpey (1941, fig. 18) is much more inflated and without a funicle compared with our high-spired form. A search of the literature failed to produce an illustration of a species which would accommodate the higher spired forms.

SPECIMENS: 26 (low-spired), 8 (high-spired).

MEASUREMENTS: AMNH 40857: H 10.0, W 18.1 mm.; AMNH 40858: H 1.7 mm.; W 2.3 mm.; AMNH 40859: H 2.0 mm., W 2.1 mm.

GENUS *TURBINILOPSIS* DE KONINCK, 1881

TYPE SPECIES: *Turbinilopsis inconspicua* de Koninck, 1881; SD Cossmann, 1916.

Turbinilopsis rotunda Delpey, 1941

Turbinilopsis rotundus Delpey, 1941, p. 276, fig. 19.

DISCUSSION: Five immature specimens can be referred to this species. They differ from the illustration of Delpey by having the outer whorl face more nearly vertical so that the last whorl has a modified tabulate appearance. The apertures are not complete but they do not seem to have as much reflection of the inner lip as does the type. The specimens are too badly preserved and too small to photograph and are mentioned here solely for the record.

SUPERFAMILY PSEUDOPHORACEA

FAMILY PSEUDOPHORIDAE S. A. MILLER, 1889

GENUS *SALLYA* YOCHELSON, 1956

TYPE SPECIES: *Sallya linsa* Yochelson, 1956, p. 205, pl. 22, figs. 1-7.

Sallya terendaka, new species

Figures 12a, 12b

DIAGNOSIS: Conical, coarsely ornamented shells with dominant, noded, prosocline ribs; protoconch unknown; early whorls absent, presumably sealed off by septa; whorl face either flat or slightly convex; axially directed cords with elongate interference nodes, cords normal to growth lines; six or more spiral threads per whorl, faint axial threads in late ontogeny forming diamond-shaped nodes on axial cords; short well-developed flange extends beyond periphery; base flat to gently convexo-concave with 10 or more spiral threads alternating with finer threads; circumumbilical ridge surrounds a narrow umbilicus with spiral threads extending into umbilicus; parietal surface unknown.

DISCUSSION: The most conspicuous and unique character of *S. terendaka* is the strongly developed and rounded cords which are essentially normal to growth lines. Each cord is contiguous with the cord in adjacent whorls, giving the appearance of continuous cording. The result of the above arrangement is a very unusual ornament pattern not seen in many Paleozoic genera. As Yochelson (1956, p. 251) in discussing the type species stated, "Because of the interruption of the revolving lirae by growth lines into short segments, at first glance specimens seem to have obliquely arranged ridges sweeping forward down the shell"; *Sallya terendaka* has exaggerated this feature. In addition, the prosocline ribs have elongated nodes with their axes parallel to the growth lines. By following a suite of nodes downward, it is possible to trace the growth track. This is necessary on some specimens since growth lines between ribs can be seen only intermittently.

Sallya linsa has weaker and discontinuous prosocline ornament formed of elongated nodes normal to the growth increments. *Sallya terendaka* is coeloconoid rather than being cyrtoconoid as in the type species. *Sallya linsa* has much more regular spiral threading on the base and appears to have a funicle. *Sallya striata* Yochelson, 1956, has very heavy cording which is parallel to the axis and is straight rather than being curved (to follow the normalcy of the curved growth lines) as in *S. linsa* and *S. terendaka*. The flanges of the other described species are more fully developed than in this species.

The protoconchs of all species of *Sallya* are missing and Yochelson (1956, p. 250) was of the opinion of that the protoconch may have been depressed or discoidal. However, the floor of the broken early whorl swings abruptly upward in the holotype of *S. terendaka* suggesting the presence of a septum. Septa are frequently found in the euomphalids, and a septum is present in the Upper Paleozoic pleurotomarian genus *Luciella* de Koninck, 1883, which is also characteristically found with the earliest whorls missing. Since the shell is not unusually long, the organism perhaps sealed off the earliest whorls to entrap gas or fluids. *Sallya* is known only from the west Texas region and now Malaysia, hence the range is extended into the lower to upper Permian.

SPECIMENS: 2.

MEASUREMENTS: Holotype AMNH 40859: SP ANG 70 degrees, H 14.0 mm., W 10.8 mm.; Paratype AMNH 40860: SP ANG 69 degrees, H 18.2 mm., W 21.3 mm.

ETYMOLOGY: Terendak, the Malaysian conical sun hat.

SUPERFAMILY CRASPEDOSTOMATACEA

FAMILY CRASPEDOSTOMATIDAE WENZ, 1938

SUBFAMILY DICHOSTASINAE YOCHELSON, 1956

GENUS *DICHOSTASIA* YOCHELSON, 1956

TYPE SPECIES: *Dichostasia complex* Yochelson, 1956, p. 267, pl. 23, figs. 12-15.

DISCUSSION: This genus, along with such other members of the family as *Brochidium* Koken, 1889, and *Temnospira* Perner, 1903, has some features unusual for marine archeogastropods. They have planar, holostomous apertures which develop an appreciable thickening of the rim of the adult stage. This thickening consists of a series of closely packed, laminar growth increments. The apertural plane is nearly vertical or parallel to the axis. In addition, they tend to have well-developed collabral ribbing and/or noding and they are low-spired and widely phaneromphalus. The thickened aperture type is usually found among the pulmonate gastropods. It is for these features that the craspedostomatids had been placed by Knight, Batten and Yochelson, (1960) in the archeogastropods with a query. However, their low-spired shape and the heavy collabral ribbing is similar to that of some members of the trochid Cyclostrematidae such as *Munditiella* Kuroda and Hare, 1954, or *Coronadoa* Bartsch, 1946. I will, therefore, tentatively place the superfamily in the order Trochina.

Dichostasia kampara, new species

Figure 13a, 13b, 13c

DIAGNOSIS: Small, low-spired, subquadratic trochiform shells with a thickened adult aperture; early whorls planispiral to somewhat depressed, lacking ornament; upper whorl surface almost horizontal, convexo-concave, one or two noded spiral cords adjacent to suture; one or more spiral threads between cords and upper margin of outer whorl face; large noded keel on shoulder composed of multiple fine threads; outer whorl face vertical, slightly concave with a noded medial spiral rib; peripheral noded rib less well developed than shoulder keel; collabral threads form nodes at intersection of spiral ornament; base flat with six or more noded spiral cords; widely phaneromphalus.

DISCUSSION: This species agrees well with the generic characters by virtue of the orthocline nature of the aperture, thickening of the aperture at maturity, the lack of ornament on the early whorls, the planispiral nature of the early whorls, the discoid to trochiform shell shape and the heavy ribbing and noding. There is little variation to record among the specimens in the Malaysian sample except for the degree of spiral element noding and the number of spiral threads present. The degree of collab-

ral ornament appears to vary in development between specimens, but the preservation is poor and this observation may not be entirely correct.

Dichostasia kampara differs from *D. complex* in having a flattened upper whorl surface and base, in having an almost vertical outer whorl face, in having more fully developed collabral ornament, more compact noding on the upper surface of the whorl, and with more numerous spiral threads. *D. simplex* Yochelson, 1956, has closely spaced, heavy collabral noding on the upper whorl surface and base and has but a single rib located on the periphery. *Discotropis* Yochelson, 1956, is also low-spired with a peripheral keel and a wide umbilicus. However, it possesses a typical sigmoid growth pattern found in the omphalotrochids. Yochelson (1956, p. 203) tentatively assigned *Euomphalus solariformis* Delpey, 1942, and *E. turritus* Delpey, 1942, to *Discotropis*. It is difficult to be sure of the growth line characteristics from the illustration of Delpey (p. 264, fig. 6), but if the drawing is correctly rendered, *E. solariformis* lacks the sigmoid growth lines of the omphalotrochids and should be accommodated in *Dichostasia*. *E. turritus* and perhaps *E. klobukowskii* Mansuy, 1912 (Delpey, 1942) should remain in the genus *Discotropis*.

SPECIMENS: 13.

MEASUREMENTS: Holotype AMNH 40862: SP ANG 122 degrees, H 2.1 mm., W 3.2 mm.; Paratype AMNH 40861: SP ANG 115 degrees, H 2.6 mm., W 4.3 mm.; Paratype AMNH 40863: SP ANG 112 degrees, H 2.0 mm., W 3.5 mm.; Paratype AMNH 40864: SP ANG 123 degrees, H 2.4 mm., W 3.5 mm.

ETYMOLOGY: Kampar, the Malaysian village near the Lee Mine no. 8.

SUBORDER NERITOPSINA

SUPERFAMILY NERITACEA RAFINESQUE, 1815

FAMILY NERITOPSIDAE GRAY, 1847

SUBFAMILY NATICOPSINAE S. A. MILLER, 1889

GENUS *NATICOPSIS* M'COY 1844

SUBGENUS *NATICOPSIS (NATICOPSIS)* M'COY, 1844

TYPE SPECIES: *Naticopsis phillipsii* M'Coy, 1844; SD Meek and Worthen, 1866.

DISCUSSION: *Naticopsis* is a ubiquitous genus, found in most marine faunas of the Upper Paleozoic. Gemmellaro (1889) described eight species from the Sosio beds of Sicily and Waagen reported on five species from the Salt Range Permian; some 50 species are known altogther in the Upper Paleozoic. The majority of these species are described from faunas containing a single species and indicates the problem of species recognition. Most workers who are faced with the task of identifying or describing naticopsid species are confronted with a paucity of distinguishing characteristics; the problem was reviewed by Batten (1966, p. 61) and Harper (1977, p. 134). Basically, species are recognized by shell shape and whorl profile, the degree of uncoiling, rate of whorl expansion, spire height, parietal deposits, and ornament. The latter two features have been used by some workers to distinguish species but similar details of the deposits and ornament can be found sporadically in different species making these characters less useful. However, in some faunas the same type of parietal deposit is found in every specimen and has been used to define species (Harper, 1977, pp. 134-137). Frequently, the aperture is filled in with matrix so that fewer specimens, if any, are available for study of parietal deposits. Another problem is distortion of the specimen so that the shell shape and whorl profile cannot be precisely defined.

As a result of a rather low level of character variation, there are few distinctive species and about eight morphotypes. These morphotypes are found at random worldwide, under different specific names, and are found throughout the Upper Paleozoic apparently without any particular pattern of distribution. For example, *Naticopsis wortheni* Knight, 1933, from the Pennsylvanian of the Mississippi Valley has its counterpart in *Naticopsis oncochiliformis* Gemmellaro, 1889, from the Permian Sosio beds of Sicily. The same phenomenon applies to species in the genus *Trachydomia* discussed below. During the course of this study, I have examined illustrations of most of the primary types as well as most reports of the species, and there does seem to be a tendency for forms with fairly rapid expansion rates, low peripheries, and flattened upper whorl surfaces to be

concentrated in Carboniferous faunas. Morphotypes in the Permian faunas, especially in the Tethyan faunal realm, tend to have globose shell shapes or have the periphery high on the whorl.

There have been too many species names applied to Tethyan morphotypes. This came about through general faunal descriptions by paleontologists not fully conversant with gastropods. Most illustrations of types are drawings, some of which are imaginatively rendered, or are poorly prepared and photographed. No attempt to revise the taxonomy will be made because the actual specimens should be examined first, a not inconsiderable task. Branson (1948) in his listing of Permian naticopsid species incorporated in the citations name changes, obvious objective synonyms, homonyms, and type species of invalid genera. Some names, for example, are based on steinkerns. *Naticopsis operculata* (Caneva) is not only a steinkern but is also a *nomen nudum*.

Naticopsis (naticopsis) piriformis Mansuy, 1912

Figures 14a, 14b

Naticopsis piriformis Mansuy, 1912, p. 118, pl. 21, fig. 7; Delpey, 1941, pp. 269-270, fig. 11.

DESCRIPTION: The whorl profile is evenly globose and the shell is moderately high-spired for the genus. The whorls embrace above the periphery except in the adult stage where there is some degree of uncoiling such that the sutural contact is just below the periphery. Collabral threads on the upper whorl surface may be present from the suture to about the periphery. The callus is swollen adjacent to the suture with irregular, anastomosing rugae which may extend down to the middle portion.

DISCUSSION: The distinguishing feature of this species is the roundness of the whorl. The three specimens in the Malaysian sample show the periphery located mid-whorl, marking the symmetrical nature of the curvature. The type specimen illustrated by Mansuy and the specimen illustrated by Delpey show the periphery higher on the whorl, indicating that the profile flattens out slightly on the base. The resulting shell shape is unusual among naticopsid species, most of which have the periphery high on the whorl and with somewhat flattened upper whorl surfaces. *Naticopsis wortheni* Knight, 1933, from the Pennsylvanian of the Mississippi River Valley and an undescribed species from the Crimean Permian are the only similar morphotypes of which I am aware.

SPECIMENS: 3.

MEASUREMENTS: Figured specimen AMNH 40865: AP ANG 93 degrees, H 10.3 mm., W 8.5 mm.

Naticopsis (naticopsis) khurensis Waagen, 1880

Figures 15a, 15b

Naticopsis khurensis Waagen, 1880, p. 100, pl. 9, fig. 10; Diener (1903), p. 64, pl. 3, fig. 3; Merla (1934), p. 305.

Naticopsis khoovensis Grabau, 1931, p. 358, pl. 35, figs. 2-4, 14; Grabau 1934, pl. 10, figs. 17-18.

Neritina khurensis Delpey, 1941, p. 271, fig. 13.

DESCRIPTION: Moderately low-spired unornamented shells with a modest whorl expansion rate. The sutures embrace on the upper whorl surface one-third the distance between the periphery and the suture. The whorl profile is elongated. The periphery is low on the whorl and the upper whorl surface is somewhat flattened. The callus is a thickened wash on the parietal surface and is evenly distributed. A parietal, conical tooth is situated, if present, just below the anal channel on the outer margin of the columellar lip.

DISCUSSION: This species belongs to the morphotype typified by *N. virgata* Knight, 1933, which has almost identical features as described above. The seven specimens in the sample differ from the type illustrated by Waagen in having a slightly more flattened upper whorl surface with a resulting stepped appearance of the shell. The specimen illustrated by Delpey (1941, pl. 270, fig. 13) differs in having a more rapid expansion rate and a lower shell height caused by the sutures embracing higher on the upper whorl surface. Differences between the specimens involve variation in the height of the body whorl and degree of whorl curvature.

SPECIMENS: 7.

MEASUREMENTS: Figured specimen AMNH 40866: SP ANG 70 degrees, H 13.3 mm., W 14.0 mm.

Naticopsis (Naticopsis) praealta Wanner, 1922
Figures 16a, 16b

Naticopsis praealta Wanner, 1922, p. 35, pl. 15, fig. 22.

DESCRIPTION: Relatively high-spired shells with a rapid expansion rate. The whorls embrace just above the periphery so that the shell is high-spired for the genus. The periphery is low on the whorl and the upper whorl surface is somewhat flattened. The parietal inductura is swollen into a teardrop-shaped pad near the anal notch, and is ornamented by irregular rugae.

DISCUSSION: *Naticopsis praealta* is an example of a morphotype represented by the American Pennsylvanian species, *N. judithae* Knight, 1933, and *N. shumardi* (McChesney), 1860. The distinctive features are the low periphery, flattened upper whorl surface and the relatively high-spired shell. This shell is not as high-spired as in those species such as *N. indicus* Waagen, 1880, which have elongated whorls with a high periphery. The *N. praealta* character combination is unusual for Permian species. The shell height feature is fairly common in such species as *N. piriformis* and *N. waageni* Gemmellaro, 1880. The Malaysian specimens differ from the type illustration in having a lower periphery and a greater expansion rate.

SPECIMENS: 4.

MEASUREMENTS: AMNH 40866: SP ANG 82 degrees, H 15.3 mm., W 14.0 mm.

Naticopsis (Naticopsis) tschernyschewi Yakowlew, 1899
Figure 17

Naticopsis tschernyschewi Yakowlew, 1899, p. 116, pl. 5, figs. 5, 7-8.

DESCRIPTION: Relatively low-spired shells with a rapid whorl expansion rate. Whorls embrace at about one-tenth the distance between the suture and periphery. The periphery is quite low on the whorl and the flattened upper whorl surface is the largest dimension on the shell. The anal notch is deep and narrow. As a result of the whorl shape, the aperture is teardrop-shaped. The parietal inductura is relatively thin and uniform.

DISCUSSION: The morphotype represents the opposite end of the range from that of *N. piriformis* or *N. khurensis* in having the most rapid whorl expansion rate which results in the adult whorl being elongated in profile with the low periphery. The whorl embracement adds to this low profile of the shell. This morphotype is uncommon in the Permian; I am aware of only one other similar form in the as yet undescribed West Texas Permian. The morphotype is more common in the Carboniferous, examples are *N. subovata* Worthen, 1883, from the American Pennsylvanian and *N. elongata* Phillips, 1836, from the Lower Carboniferous of England. The type specimen as illustrated in Yakowlew (1899) differs from the Malaysian specimens by being slightly higher spired with whorl embracement at about one-twentieth the distance from the suture to the periphery.

SPECIMENS: 5.

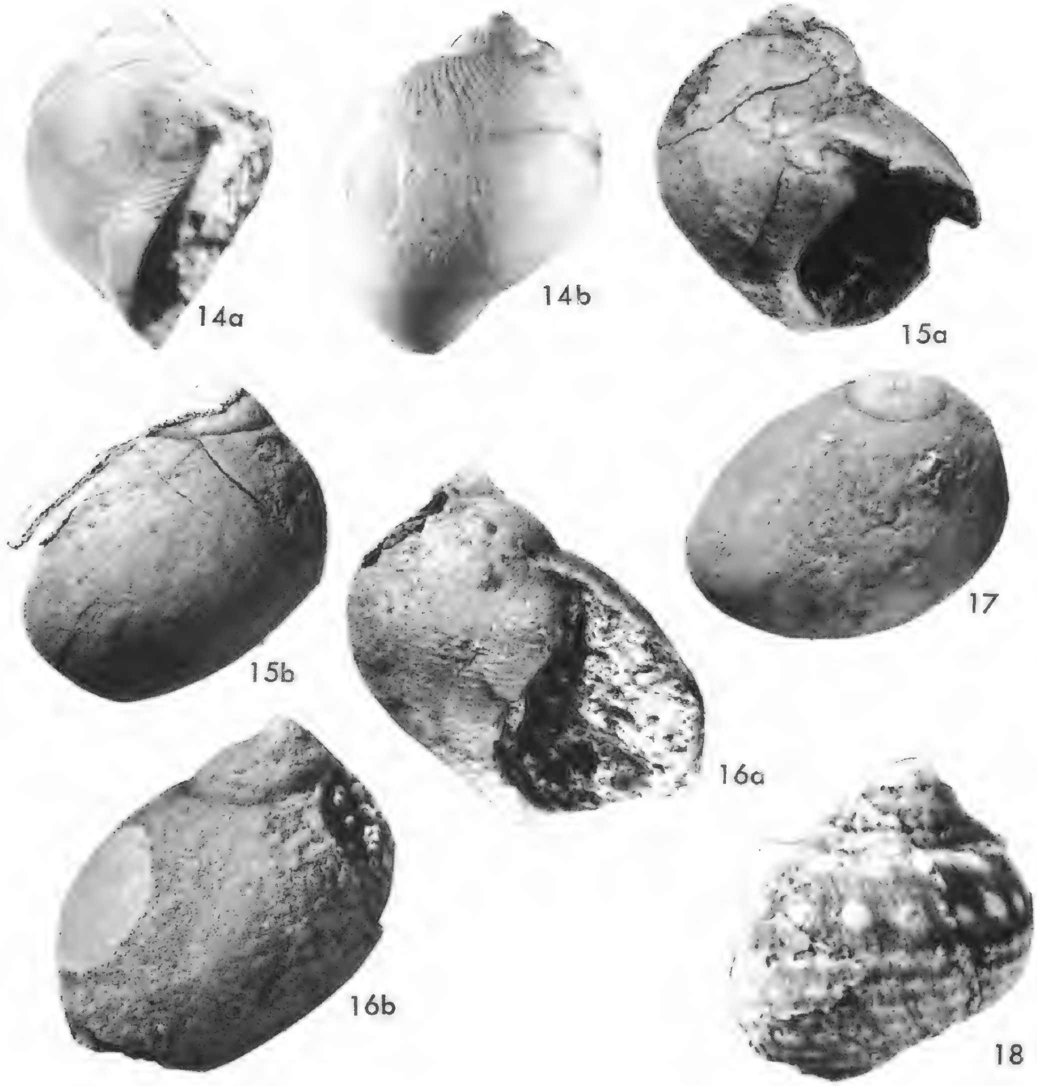
MEASUREMENTS: AMNH 40867: SP ANG 130 degrees, H 9.3 mm., W 11.5 mm.

SUBFAMILY NERITOPSIDAE, GRAY, 1847

GENUS *TRACHYDOMIA* MEEK AND WORTHEN, 1866

TYPE SPECIES: *Naticopsis nodosa* Meek and Worthen, 1861, p. 463.

DISCUSSION: Four species are recognized in the fauna as belonging to this genus. They represent distinct morphotypes which can be found elsewhere in the Carboniferous and Permian in the northern Hemisphere. One of the characteristics of the genus according to Knight, Batten and Yochelson (1960) is the presence of a narrow ramp or subsutural bank which forms an attenuated shoulder or upper whorl face. In this fauna, *T. gobbetti*, new species, and *T. imbricata*, new species, are sufficiently well represented to be able to evaluate species variation. Both species show that the ramp may or may not be present and when present it may be much broader than is usually



FIGS. 14-18. 14a. *Naticopsis (Naticopsis) piriformis* Mansuy, 1912, AMNH 40865, aperatural view, note irregular rugae on callus, X4.2. 14b. Side view, note ornament on the upper whorl surface adjacent to the suture, X4.2. 15a. *Naticopsis (Naticopsis) khurensis* Waagen, 1880, AMNH 40855, apertural view, X3.4. 15b. Side view, X3.4. 16a. *Naticopsis (Naticopsis) praealta* Wanner, 1922, AMNH 40866, apertural view, note swollen callus, X3.4. 16b. Slightly oblique side view, X3.4. 17. *Naticopsis (Naticopsis) tschernyschewi* Yakowlew, 1899, AMNH 40867, oblique side view, X3.4. 18. *Trachydomia gobbetti*, paratype, AMNH 40870, side view showing two rows of large nodes adjacent to the suture, X8.5.

found in the genus. Another characteristic is "the surface [of the whorl] covered with pustules that are not segregated sharply into different kinds" (Knight, Batten and Yochelson, 1960, p. 277). This near uniformity of pustules distinguishes the genus from *Trachyspira* Gem-

mellaro, 1889, which has two sets of pustules of different magnitude. However, in a number of described species of *Trachydomia* several rows of ornament near the suture and on the base are of different magnitude than the rows on the outer whorl face. In fact, in the Permian of West Texas there is an undescribed species which has two rows of spines near the suture with rows of nodes below.

As described below, ornament patterns are quite variable in such species as *T. gobbetti*, new species, and *T. gemmulata*, new species, giving a different complexion to the specimens. One pattern worthy of mention here is the development of quincunx ornament in several species discussed below, formed by a primary arrangement of nodes in spiral rows. These nodes are further distributed in adjacent rows in such a way that they form lineations in both a prosocline and an opisthocline direction and this arrangement over the log spiral whorl surface produces the quincunx. In most species a groove formed in the adult lower and outer lip indicates the presence, during life, of an operculum.

It is interesting to note that a modern representative of the family Neritopsidae, *Neritopsis radula* (Linné) has an apertural complex similar to *Trachyspira* and *Trachydomia*. In some populations, *Neritopsis radula* may have imbricated growth lines as in *T. imbricata*, new species, and further, has growth lines visible on the noding. The nodes of *N. radula* are rounded and arranged spirally as in most species of *Trachydomia* and they are also arranged in the opisthocline direction (see fig. 24). It is likely that *T. imbricata* or some very closely related species could be close to ancestral stock of such Triassic species as *N. ornata* Kittl, 1892.

Trachydomia gobbetti, new species

Figures 18-19a, 19b

Diagnosis: Globose shells with a sloping to concave subsutural ramp which bears from one to three spiral rows of nodes; five to eight rows of nodes, which decrease in intensity toward the base; ornament on the inflated outer whorl face; base somewhat flattened with about six rows of nodes; nodes of outer whorl face and base form quincunx pattern.

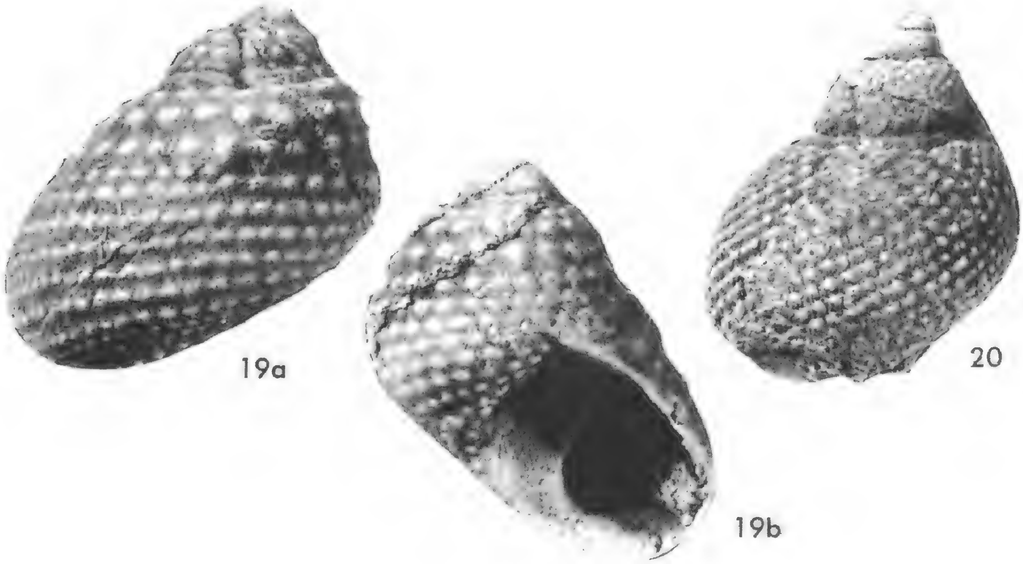
Discussion: This species belongs to a morphotype group that includes *T. whitei* Knight, 1933, *T. nodulosum* Worthen, 1884, and *T. raymondi* Sturgeon, 1964, from the Pennsylvanian of the United States. This morphotype has not previously been reported from the eastern Tethys. It differs from the other species by having a wider and more sloping subsutural ramp from one to three more rows of rounded nodes than does *T. raymondi; T. nodulosum* has smaller and more angular nodes, and *T. whitei* has fewer rows of more elongate nodes with their axes parallel to the rows.

The most obvious individual variation involves the ornament. The species is characterized by the rounded nodes arranged primarily in spiral rows. The nodes are strongest in development at the top of the outer whorl face and becomes progressively weaker toward the base. One variation of this scheme is represented by specimens having the first two or three rows with much larger nodes separated by gaps from other adjacent rows (see fig. 18). This variant has the basal rows with smaller more elongate nodes than those on the outer whorl face. Some specimens have growth increments consisting of imbricated lamellae directed adapically.

The ornament develops progressively during ontogeny with nodes becoming larger and new rows added as the whorl surface increases. However, in some specimens the node size increases rapidly, producing conspicuously large nodes but with the number of rows remaining the same until the fourth whorl where the nodes become much finer and new rows are added. Most specimens have the reverse condition with small nodes in the early whorls, followed by an abrupt change in the adult whorl to fewer rows and distinctly larger nodes in proportion to those found in the penultimate whorl.

Specimens: 22.

Measurements: Holotype AMNH 40868: SP ANG 98 degrees, H 10.0, W 10.5 mm.; Paratype AMNH 40869: SP ANG 100 degrees, H 9.8 mm., W 9.0 mm.; Paratype AMNH



FIGS. 19-20. 19. *Trachydomia gobbetti*, holotype, AMNH 40868, side view, X4.25. 19b. Apertural view, X4.25. 20. *Trachydomia dussaulti* Mansuy, 1913, AMNH 40872, side view, X3.4.

40870: SP ANG 94 degrees, H 4.2 mm., W 4.3 mm.; Paratype AMNH 40871: SP ANG 90 degrees, H 9.6 mm., W 9.6 mm.

ETYMOLOGY: Named for Derek Gobbett.

Trachydomia dussaulti Mansuy, 1913
Figure 20

Trachydomia dussaulti Mansuy, 1913, p. 101, pl. 11, figs. 5a-b; Delpey, 1941, p. 268, fig. 10.

DESCRIPTION: Shells composed of elongated globose or inflated whorls with a narrow subsutural ramp. The subsutural ramp is ornamented by relatively fine nodes at the suture. There are about 18 spiral rows which are lineated more strongly in the prosocline mode and less so in the opisthocline mode, (see fig. 20). Body whorl embraces on the base just below the periphery.

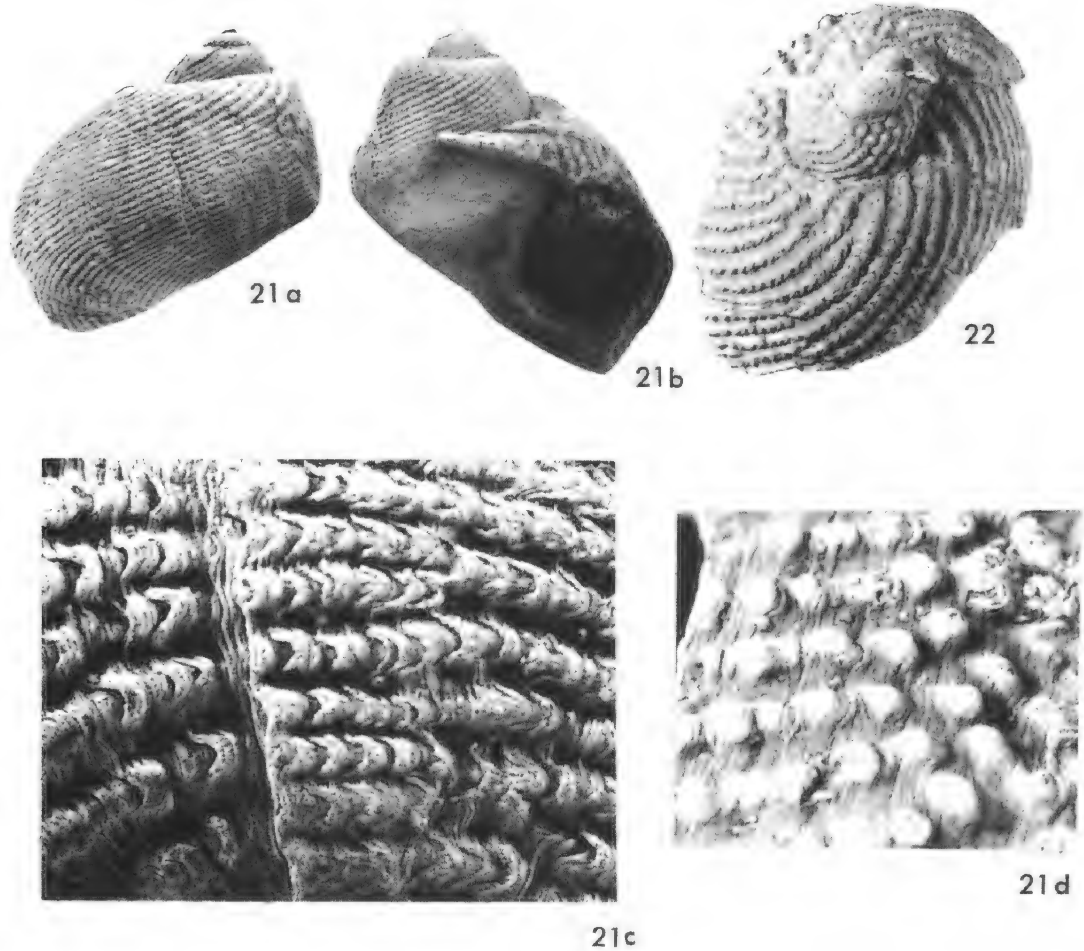
DISCUSSION: In contrast to the *T. gobbetti* morphotype, the nodes on the whorl surface are evenly developed and, except for the finer sutural nodes, are uniform in size. *Trachydomia dussaulti* has smaller nodes than *T. gobbetti* or the type species *T. nodosum*. It resembles *T. sayrei* Knight, 1933, both in the whorl profile where the periphery or area of greatest inflation is low and in the size and distribution of the nodes. The two Malaysian specimens differ from Mansuy's type in having slightly finer node development and being higher-spired; they appear very close to the specimen illustrated by Delpey from Phnom Takream, Cambodia. The type specimens were described by Mansuy from Kham-mon, Tonkin, Viet Nam.

SPECIMENS: 2.

MEASUREMENTS: Figured specimen AMNH 40872: SP ANG 72 degrees, H 13.5 mm., W 11.2 mm.

Trachydomia imbricata, new species
Figures 21-26

DIAGNOSIS: Globose shell with pendant shaped whorls; imbricated ribs or rows of nodes arranged in opisthocline orientation, prosocline growth lines imbricated.



FIGS. 21-22. 21a. *Trachydomia imbricata*, holotype, AMNH 40873, side view showing low, rounded periphery, X.85. 21b. Apertural view, X. 85. 21c. Details showing half-dome nodes near suture, X6 (approx.). 21d. Detail showing rounded node development, X7.6 (approx.). 22. Paratype, AMNH 40874, oblique top view showing prosocline ribbing, X1.75.

DESCRIPTION: The globose whorls have a sloping outer whorl face which ranges from an almost flat to a rounded surface. A broad periphery low on the whorl may not be defined if the whorl is rounded. The sutures embrace at or just below the periphery causing a variety of shell shapes, ranging from high-spired, when sutures are low on the periphery, to globose. The subsutural ramp is narrow and may have a row of nodes or imbricate structure less well developed than that on the rest of the whorl.

Growth lines are frequently imbricated, feathery and somewhat irregularly spaced. The ornament is primarily oriented in the prosocline direction and is essentially normal to the opisthocline growth lines. The ornament ranges from slightly raised U-shaped half-dome imbrications on ribs to discrete, rounded nodes. On a few specimens, the earlier whorls have a quincuncial pattern of nodes but all adult whorls are opisthocline only. Growth lines are complete over the nodes, a condition not noted in other species. The nodes, if developed, are usually finer on the base except at the edge of the parietal surface where one or two rows may have stronger noding.

DISCUSSION: The morphotype represented by this species is another distinctive group within

the *Trachydomia*. The three morphotypes involving ornament are *T. imbricata*, new species, which has dominant opisthocline ornament, *T. moorei* Knight, 1933, which has a dominance of spiral ornament and *T. nodulosum* Worthen, 1884, which has prosocline ornament. Of the 49 specimens in the sample, 14 specimens have discrete, rounded to elongate nodes (see fig. 21d). The rest have imbricated half-dome protuberances which are formed from upraised growth lines. These structures, in turn, form a more or less continuous rib, (see fig. 22). They may be barely raised above the surface at about the same interval as those that are more strongly developed, and are usually more numerous than nodes.

I have observed this type of ornament pattern or imbricated growth line feature in only one other described species, that illusträted as *T. tuberculata-lineata* Renz, (1940, pl. 11, fig. 9), from Karakorum, and considered it to be a syntype. This species has fine nodes which appear to be developed over the whorl; the nodes, while primarily alligned spirally, have a secondary opisthocline lineation. The whorl shape and height of spire appears similar to *T. imbricata*. The specimen illustrated on pl. 11, fig. 9 is here designated the lectotype and fits easily into the *T. nodulosum* morphotype. Two other illustrated paratypes (Renz 1940, pl. 11, figs. 7, 8) are noded with finer nodes near the suture and on the base. Another similar form is a single specimen from the Permian of West Texas which has the same ornament as the noded variant in this sample.

An imbricated growth pattern is found in several species of *Trachyspira* Gemmellaro, 1889 for example, *T. sturi* (Gemmellaro, 1889).

SPECIMENS: 49.

MEASUREMENTS: Holotype, AMNH 40873: SP ANG 120 degrees, H 47.4 mm.; W 52.0 mm. (broken); Paratype, AMNH 40875: SP ANG 87 degrees, H 21.6 mm.; W 23.5 mm.; Paratype AMNH 40877: SP ANG 96 degrees, H 16.6 mm., (broken); W 16.0 mm.; Paratype AMNH 40878: SP ANG 102 degrees, H 27.8 mm., W 26.7 mm.

ETYMOLOGY: From the Latin *imbrex* overlapping, like roofing shingles.

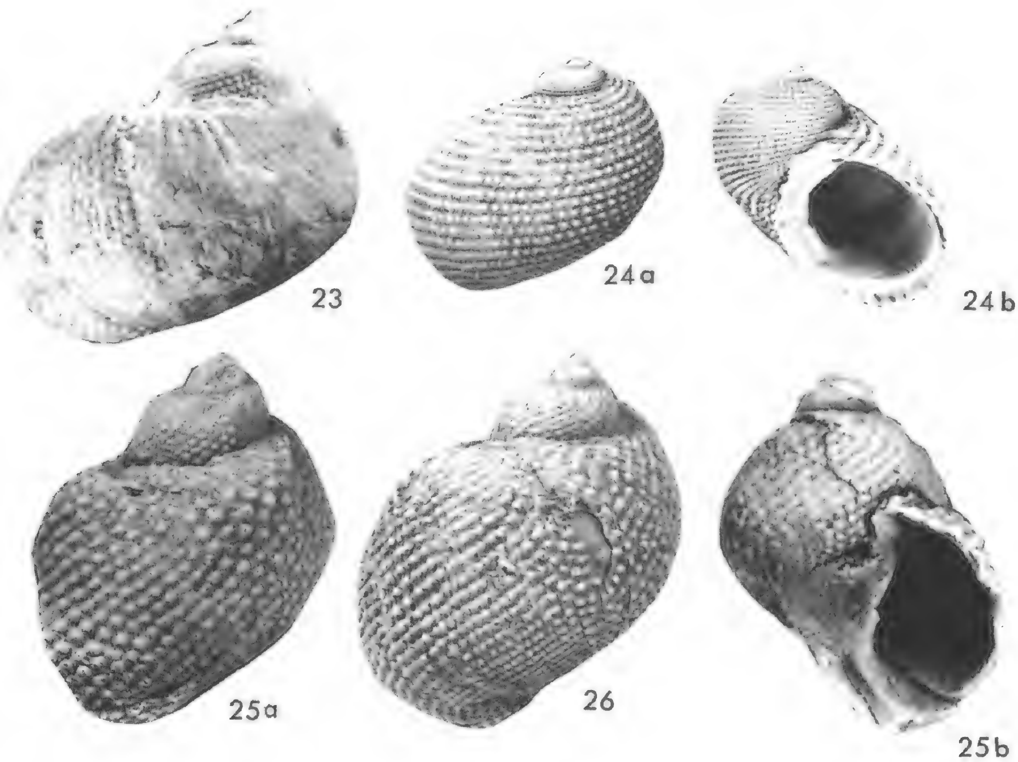
Trachydomia gemmulata, new species

Figures 27-28

DIAGNOSIS: Relatively high-spired, subtrochiform shells with a few rows of large nodes arrange quincuncially; flattened subsutural ramp sloping outward; eight or more rows of nodes with basal rows not well developed; sutures embrace below periphery; upper whorl surface somewhat flattened.

DISCUSSION: This species represents one extreme of the morphotype range. The very large nodes are far fewer in number per surface area compared to any other species of *Trachydomia*. There are also fewer rows so that the quincunx pattern is not as obvious as in *T. gobbetti*, for example. The rows on the base are closer together and the nodes are smaller and more numerous. On one specimen the rows near the suture have nodes which are pointed and almost spinose. As in *T. imbricata*, the growth lines cross the nodes.

This species belongs to the same morphotype as *T. moorei* Knight, 1933; both have three rows of nodes on the upper whorl surface with the same shape and arrangement of the nodes. The whorl profile differs from that of *T. moorei* by being more tabulate, also the nodes are more elongate in the spiral direction. *Trachydomia gemmulata* is quite distinct and is unknown elsewhere in the Permian with one possible exception; Merla (1931) identified a specimen from the Bellerophonkalk of the Dolomite Alps as belonging to *Trachynerita ambigua* Caneva, 1906, which probably can be assigned to *T. gemmulata*. *Trachydomia ambigua* (Caneva) probably belongs to the morphotype represented by *T. gobbetti*, but the illustration of the type is not presented well enought to be certain. The Bellerophonkalk specimen is described as having several rows of large nodes which appear to be restricted to the upper whorl surface. The illustration rendered by Merla *(op. cit.)* is a stylized pencil sketch and is difficult to decipher; however, it is unlikely that a species of *Trachydomia* would have such a restricted type of ornament and much more likely that the specimen is poorly preserved. This species comes closest to *T. tuberosa* Wanner, 1942, from Panukat, Timor,



FIGS. 23-26. Paratype, AMNH 40875, side view showing a more compressed whorl profile, X1.75. 24a. *Neritopsis radula* (Linné), AMNH 40876, side view, X1.3. 24b. Apertural view, X1.3. 25a. *Trachydomia imbricata*, paratype, AMNH 40877, slightly oblique side view showing rounded nodes and a flattened whorl profile, X1.75. 25b. Apertural view, X1.7. 26. *Trachydomia imbricata*, paratype, AMNH 40878, side view, X2.5.

which has large, identical nodes that are fewer in number per row and alternate in adjacent rows in a random pattern. The whorl of *T. tuberosa* is much more globose and the subsutural ramp is narrow and sharply defined. The nodes on the penultimate whorl are much reduced.

The three specimens of *Trachydomia gemmulata* are much larger than *T. tuberosa* or any other species of *Trachydomia* that I have seen. Finally, the three specimens are imperfect, being broken and distorted.

SPECIMENS: 3.

MEASUREMENTS: Holotype AMNH 40879: SP ANG 96 degrees, H 36.7 mm., W 38.4 mm.; Paratype AMNH 40632: SP ANG 105 degrees, H 28.0 mm., W 34.4 mm.; Paratype AMNH 40633: SP ANG 94 degrees, H 34.0 mm., W 39.0 mm.

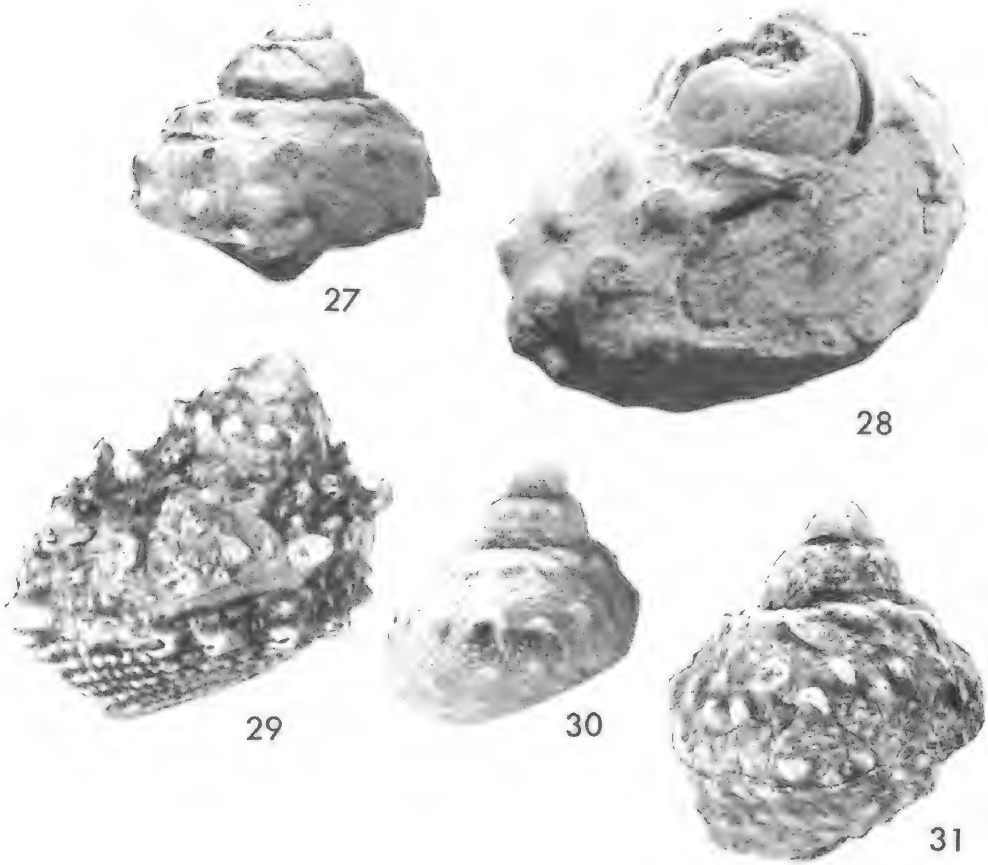
ETYMOLOGY: Gemmulata, derived from the Latin *gemma*, bud, eye, or jewel.

GENUS *TRACHYSPIRA* GEMMELLARO, 1889

TYPE SPECIES: *Trachyspira delphinuloides* Gemmellaro, 1889; SD Cossman, 1916.

DISCUSSION: One of the principal characters heretofore used to distinguish *Trachydomia* from *Trachyspira* is the presence of a subsutural ramp. The ramp is absent in many specimens representing species in both genera, a point not previously observed, rendering this feature useless for generic separation.

The whorl profile in the type species de-



FIGS. 27-28. 27. *Trachydomia gemmulata*, holotype, AMNH 40879, side view, X1. 28. *Trachydomia gemmulata*, paratype, AMNH 40880, oblique side view, X1.5.
FIGS. 29-31. 29. *Trachyspira delphinuloides* Gemmellaro, 1889, AMNH 40881, side view of specimen from the Permian of Djebel Tebaga, Tunisia showing imbricate spines and nodes, X4. 30. *Trachyspira delphinuloides*, AMNH 40882, Lee Mine no. 8, side view, X1. 31. *Trachyspira delphinuloides*, AMNH 40883, Lee Mine no. 8, side view, X1.

scribed by Gemmellaro (1889) and redescribed by Greco (1937) is inflated but somewhat stepped owing to the upper whorl surface and the relative emphasis of the rows of nodes. There are several exceptions to this type of whorl profile as in *T. canaliculatus* Gemmellaro, 1889, which has an evenly globose profile with three rows of elongate nodes which are not well developed and disappear in the gerontic stage. *Sosiospira gemmellaroi* Greco, 1937 is quite similar in shape to *T. canaliculatus* although the rows of nodes are confined to early ontogenetic stages. *S. gemmellaroi* is considered a subjective synonym of *T. canaliculatus*, which was subsequently designated the type species of *Sosiospira* by Knight (1945). Knight, Batten and Yochelson (1960, p. 277) concluded that *Sosiospira* was a subjective synonym of *Trachyspira*. *Sosiospira* is known from the Sosio beds and the characters used to distinguish it (a smoothly globose whorl profile, a rapidly expanding whorl and a neritid shell without nodes in adult stages) from *Trachydomia* and *Tra-*

chyspira are no less significant than those used to separate those genera. This study suggests that *Sosiospira* and *Trachyspira* should be considered as synonyms of *Trachydomia*. However, such action is not warranted until the species described from Sosio are re-examined in light of their being a portion of a broad spectrum of variation and until better specimens are found in southeastern Asia.

The two important characters used in recognizing the species of *Trachyspira* are the ornament pattern and the whorl profile. *Trachyspira acanthica* Gemmellaro, 1889, for example, has a row of nodes located at the edge of a somewhat flattened upper whorl face. *T. armata* Greco, 1937, has two rows of nodes; the lower row is dominant, forming the margin of the base and the upper whorl face. The outer whorl face is slightly flattened. *Trachyspira delphinuloides* has three rows of nodes with the second row dominant (see discussion of that species). *Trachyspira inermis* Greco, 1937 has a similar ornament pattern as *T. acanthica*. *Trachyspira milligranum* Gemmellaro, 1889, also has three rows of major nodes of which the upper two rows are equal in development, but with the third row on the base. *Trachyspira canaliculatus* has three equally well-developed rows of nodes on a globose whorl.

Trachyspira is known only from the Middle Permian in southern Tunisia, Sicily, Malaysia, and West Texas; the majority of the species are known only from Sicily, and the assumption is made that Sicily was the possible center of dispersal and probable place of origin. *Trachydomia*, on the other hand, is widespread in Eurasia and North America from early Pennsylvanian through the middle Permian. The shape, size, and numbers of small nodes in most species of *Trachydomia* indicates that they may be homologous to the pustules of *Trachyspira* rather than the nodes. This is particularly so for the type of node and growth increments seen in *Trachydomia imbricata*, new species (see figs. 21c, d). The larger nodes found in such species of *Trachydomia* as *T. gemmulata*, new species, or *T. moorei* Knight, 1933, may be homologous to the nodes in *Trachyspira* because the rows of nodes vary in similar manner, that is, one row of nodes may be more fully formed than others or the number of rows may vary.

In brief, all ornament features of *Trachyspira* are present in *Trachydomia* in addition to shell shape variation, ramp detail, whorl profile detail, sutural embracement variation, and apertural details. The only characters apparently now separating the two genera is the combination of the two orders of nodes, (the pustules and nodes) found in *Trachyspira* and the single order of nodes in *Trachydomia*. However, individual specimens of *Trachydomia gemmulata*, new species, *Trachydomia gobbetti*, new species, and *Trachydomia moorei* show nodes which vary in size. Hence there is a genetic potential for the combination of these "generic" characters in a single species.

There appears to be two end-member groups of species in these two closely related genera (there are some 20 species of *Trachydomia* and six of *Trachyspira*). The Malaysian specimens indicate that there is considerable overlap between the two genera based on ornament alone. However, an additional character that should be considered in making a taxonomic decision is the presence of a thick complex prismatic layer and a thin outer simple prismatic layer in the shell of *Trachydomia* cf. *T. nodosum* (Meek and Worthen), 1861, from the Bend group of Texas. One of the specimens of *Trachyspira delphinuloides* in our sample has a very thick shell composed of a single layer of complex prisms, similar to those found in *Shansiella carbonaria* (Norwood and Pratten), 1855, reported by Batten (1972, fig. 6) or *Bellerophon* Montfort, 1808, (see MacClintock, 1967, pp. 94-107). Prism terminations in growth increments are raised above the shell surface forming growth lines so that no other layer is possible (fig. 32). The prisms of *Trachydomia nodosum* are finer in proportion to their length than in *Trachyspira delphinuloides* and there is a thin outer layer. *Neritopsis radula*, the single extant species of the subfamily, is significantly different in ultrastructure from both species in having two crossed-lamellar layers (see fig. 33). In conclusion, the undescribed neritids from the West Texas Permian should be analyzed and the neritids from Sicily and Djebel Tebaga should be restudied before a final decision regarding the taxonomic status of the two genera can be made.

It should be noted that the subfamily is quite

conservative with six genera that range from the Lower Carboniferous to Recent. *Trachydomia* and *Trachyspira* are the most diverse genera, the others being represented by just a few species. *Neritopsis*, for example, which first appeared in the Middle Triassic, is represented by a few conservative, long-ranging species such as the extant *N. radula* which has remained essentially unchanged since its appearance in the Eocene.

Trachyspira delphinuloides Gemmellaro, 1889
Figures 29-32

Trachyspira delphinuloides Gemmellaro, 1889, p. 150, pl. 13, figs. 14-16: Termier, Termier and Vachard, 1977, p. 70, fig. 24.

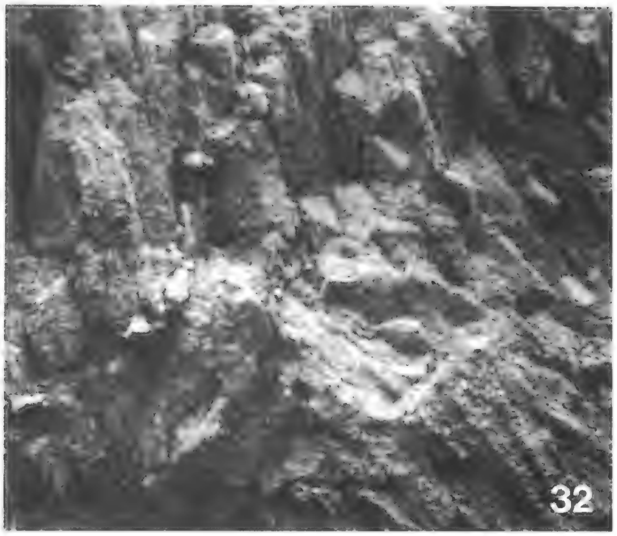


FIG. 32. *Trachyspira delphinuloides*, AMNH 40884, a cross section of the mid-whorl; the complex prisms are oblique downward and parallel to the growth increments, X22.

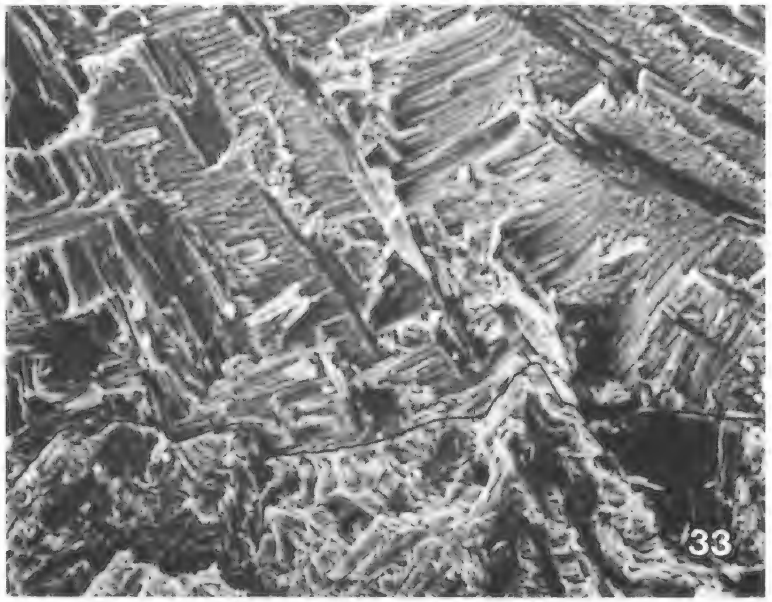


FIG. 33. *Neritopsis radula* (Linné), 1758, AMNH 40885, a cross section of the mid-whorl; the section is oriented in the spiral direction so that the first order lamellae of the inner layer parallel to the view. The outer layer is the lower layer marked by the irregular boundary line in the lower part of the micrograph, X235.

DESCRIPTION: Subtrochiform shells with a somewhat flattened upper whorl surface which may slope downward and outward. The growth increments are slightly lamellose or imbricated. The subsutural ramp, when present, is usually concave and unornamented. There are three rows of nodes; the uppermost forms the boundary between the subsutural ramp and the upper whorl surface. The medial row of nodes usually forms the boundary between the upper whorl surface and the outer whorl face. The third row of nodes is on the upper portion of the base, or in some specimens, it forms the boundary between the rounded base and outer whorl face. The upper and outer whorl faces may be flat to concave, however, the whorl profile has a globose aspect (see fig. 30). In some specimens an extra row of nodes slightly less well developed than the three principal rows may appear immediately below a boundary row and is slightly offset along the opisthocline lineation (see fig. 31). There may be two to four rows of nodes on the base which are weaker than those on the rest of the whorl. On some specimens these basal rows may be absent or very weak. These nodes tend to be round but may be elongated in the spiral direction.

There are numerous pustules which are placed in spiral rows but are quincuncially arranged with a stronger emphasis on prosocline lineation. The pustules are absent on the ramp, but found faily uniformly over the surface of the shell between node rows. The imbricated growth increments can be traced over the nodes and pustules. The first and second node rows are dominant with the second row usually more fully developed and even spinose in many specimens. In some specimens the two rows may be equally well formed.

DISCUSSION: Each of the 12 Malaysian specimens studied shows some variation of the patterns described above. For example, in one specimen the three rows are equally developed, another specimen has the upper two rows stronger, whereas in five specimens the second row is strongest. On two specimens there are no rows of nodes on the base. Another specimen has a few random pustules with no particular overall pattern; in this case preservation is perfect and the growth increments indicate that the pustules failed to form. One specimen has quite large pustules which are fewer in number, and finally, one specimen lacks pustules entirely but has the characters of the species. This variation is consistent with patterns used in the past to differentiate species, as mentioned in the generic discussion.

This Malaysian sample is sufficiently similar to *T. delphinuloides* from the Mediterranean region to justify placement in the species. However, there are some striking differences which are not apparent from the illustrations of Gemmellaro (1889), Termier, Termier and Vachard (1977), and Knight (1945). A sample of 19 specimens from the Permian (Sosio equivalent) at Djebel Tebaga, southern Tunisia, shows that the growth increments are raised lamellose sheets which are imbricated (see fig. 29). The pustules may be formed by a progressive rise in the growth sheets in the shape of an open half-dome or, in some areas of the shell, may be rounded nodes with growth increments crossing over the face. The nodes are growth sheets raised into hollow spines which may be partially open, (see fig. 29). On most specimens that are worn the spines appear as solid ovoid or teardrop-shaped nodes, or even rounded nodes (see fig. 24, p. 70 of Termier, Termier and Vachard, 1977). Most illustrations in the publications cited above show such worn specimens, including the presumed holotype illustrated by Knight (1945). The imbricated or lamellose growth increments and specialized nodes and pustules described above are commonly found in the subfamily, including *Neritopsis radula* (Linné), 1758.

The second spine row of *T. delphinuloides* from Tunisia is strongest and with longer spines, with the third row next strongest. The first row which forms the margin of the subsutural ramp is not developed at all on several specimens. The pustules are formed exclusively in the prosocline lineation in the Tunisian sample, whereas they form along the sprial lineation in the Malaysian sample. The Malaysian sample averages markedly larger and higher-spired (with means of SP ANG 76 degrees, H 35.2 mm., W 33.6 mm) than the Tunisian sample (with means of SP ANG 82 degrees, H 21.5 mm., W 20.55 mm). The lower spiral

angle of the Malaysian sample indicates that the whorls embrace lower on the base than the Mediteranean material. The most striking difference, however, is the wide range of variation in the spiral node rows in the Malaysian sample. Without studying the type material of the five Sicilian species (*T. acanthica* Gemmellaro, 1889, *T. armata* Greco, 1937, *T. delphinuloides* Gemmellaro, 1889, *T. inermis* Greco, 1937, and *T. millegranum* Gemmellaro, 1890) it is not possible to test the hypothesis that these species represent but a single variable species, *T. delphinuloides*. The ornament character array in the Malaysian sample contraindicates the presence of any other Sicilian species in southeast Asia.

SPECIMENS: 12.

MEASUREMENTS: Figured specimens, AMNH 40634: SP ANG 75 degrees, H 12.2 mm., W 11.0 mm.; AMNH 40635: SP ANG 74 degrees, H 43.6 mm., W 37.1 mm.; AMNH 40636: SP ANG 73 degrees, H 34.9 mm., W 33.8 mm.

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